

DISTRIBUTION, ECOLOGY AND EVOLUTION
OF THE BELLBIRDS
(*PROCNIAS*, COTINGIDAE)



BY
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DISTRIBUTION, ECOLOGY AND EVOLUTION OF THE BELLBIRDS (*PROCNIAS*, COTINGIDAE)

By D. W. SNOW

THE four species of bellbirds of the genus *Procnias* constitute one of the most peculiar of the many isolated genera placed in the suboscine family Cotingidae. This New World family, of mainly tropical distribution, is so diverse that it might well be subdivided into several families if there appeared to be any reasonable way of doing so. The recent studies of Ames (1971) and Olson (1971) show, however, that the anatomical characters that have been used to distinguish the higher categories of suboscine birds are distributed in a most confusing pattern among the cotingid genera, and it would be premature to attempt a full revision at the higher systematic levels until a better understanding of these and other characters has been attained. It is at least clear that many of the cotingid genera are of ancient origin, though it is not known whether the modern genera are a remnant of a much greater variety of forms, of which many have become extinct, or whether the evolution of the family has been concentrated along those phyletic lines which are still alive today.

In a family consisting largely of frugivorous forest birds, the bellbirds are perhaps the most specialized fruit-eaters of all. The only detailed field study, of *Procnias averano* in Trinidad (Snow 1970), showed that the adults not only feed entirely on fruit themselves but feed the young on fruit alone. They have short bills, very broad at the gape, which give the head an almost frog-like appearance and enable them to swallow whole relatively very large fruits. In this respect they are closely paralleled by the broadbill genus *Calyptomena* (Eurylaimidae) of the oriental region (Olson 1971), while the other medium-sized fruit-eating cotingas (e.g. *Cotinga*, *Xipholena*) show this beak form in less extreme degree. Like other cotingas, bellbirds typically pluck their food in flight.

In common with some other fruit-eating forest cotingas – and in parallel with the birds of paradise (Paradisaeidae) of the New Guinea region – the bellbirds have evolved extreme sexual dimorphism. The males of the four species are superficially very distinct, being ornamented in strikingly different ways with wattles or bare areas of skin. Two of them are among the very few species of land-birds with wholly white plumage. The females, on the other hand, are very alike, being olive-green above and pale yellowish with longitudinal streaks below. They are considerably smaller than the males – 85–89 per cent by wing-length, and about 71 per cent by weight in *P. nudicollis*, the only species for which an adequate series of weights is available (Table 1). The males spend much of their time in epigamic display, making themselves conspicuous by uttering extraordinarily loud explosive calls from high perches. At close quarters, visual displays are combined with calls. Snow (1970) gives a detailed account of the behaviour of the Bearded Bellbird, *P. averano*,

and short accounts of *P. alba* and *P. tricarunculata* have been given by Snow (1961) and Skutch (1969) respectively.

TABLE I

Wing-measurements of males and females of the four species of *Procnias*

		N	Range	Mean
<i>P. averano</i>	adult males	8	152-163	158.5
	immature males	9	146-161	155.0
	females	6	133-142	138.3
<i>P. nudicollis</i>	adult males	24	151-164	156.7
	immature males	51	144-162	154.0
	females	41	130-149	139.1
<i>P. alba</i>	adult males	13	155-170	161.0
	immature males	6	156-163	160.0
	females	11	131-140	136.4
<i>P. tricarunculata</i>	adult males	39	160-175	165.5
	immature males	16	155-171	163.4
	females	13	136-152	145.1

Notes. Measurements of *P. averano* are for the Venezuelan and Trinidad population; N.E. Brazilian birds apparently do not differ appreciably in size.

Sexing of birds in female plumage is sometimes unreliable in the older collections. One specimen of *P. alba*, labelled female, with a wing of 159 mm is omitted since it is almost certainly wrongly sexed.

Weights of *P. nudicollis*: 3 adult males, 177-225 g (average 199); 5 immature males 168-201 g (average, 184); 5 females, 120-150 g (average, 142).

The complete synonymy of the genus, with all previous important literature citations and distributional records, was given by Hellmayr (1929), since when no new form has been described and no major extension of range recorded.

RELATIONSHIPS WITHIN THE GENUS

The four species are illustrated in Figure 1. This drawing shows the conspicuous differences between the species, but does not indicate the less conspicuous resemblances between them, on the basis of which it is fairly clear that they fall into two closely related pairs, *P. averano* and *P. nudicollis* on the one hand and *P. alba* and *P. tricarunculata* on the other. Each of these pairs has a number of characters in common, and there is little doubt that the genus in its present state has arisen from an original splitting of an ancestral form into two species, followed by a further splitting of each.

P. averano and *P. nudicollis*. In the adult male the throat is bare or furnished with rudimentary black feathers; there is a bare patch of skin on the side of the femur; and the modified tips of the outer primaries (Figure 2) are somewhat

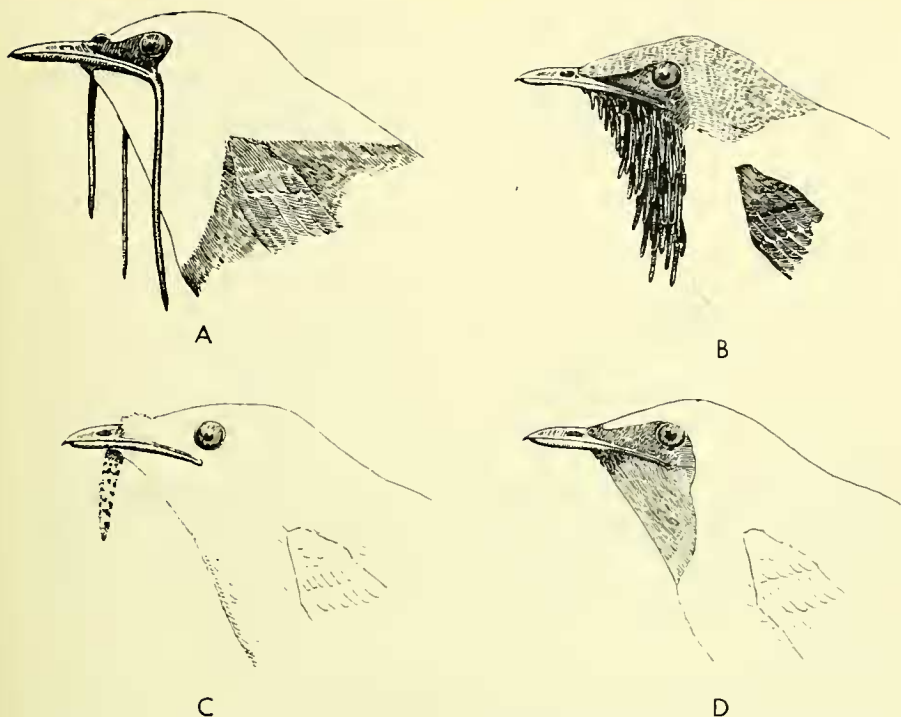


FIG. 1. Adult males of (A) *Procnias tricarunculata*, (B) *P. averano*, (C) *P. alba*, (D) *P. nudicollis*. Colour of plumage as follows: *P. tricarunculata*, head white, rest of plumage chestnut brown; *P. alba* and *P. nudicollis*, all white (bare skin of face and throat greenish in *P. nudicollis*); *P. averano*, top of head coffee-brown, wings black, rest of plumage very pale grey in western population, white in northeastern Brazilian population.

alike. In the juvenile male, the crown passes through an intermediate sooty-black stage before it acquires the adult colour. In the adult female, the crown is darker than the back and the throat feathers are mainly dark. These two species are almost exactly the same size, and a little smaller than the other two (Table 1).

In both species the males have two distinct kinds of call: a single short hammer-like note, and a succession of less loud, regularly repeated notes.

P. alba and *P. tricarunculata*. The adult males of both species have an elongated wattle springing from the base of the upper mandible (*P. tricarunculata* also has two similar wattles arising from the corners of the gape); the throat is feathered; there is apparently no bare patch on the femur; and the modified tips of the outer primaries are much alike in shape. The juvenile male does not develop a dark crown at any stage. In the adult female, the crown is the same green as the back and the throat is pale.

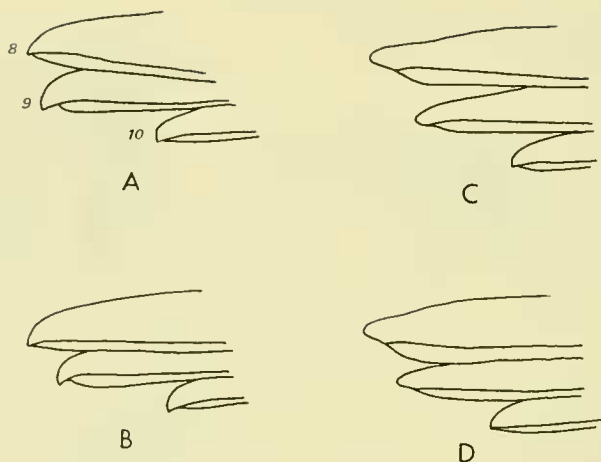


FIG. 2. Shapes of outer primary feathers in adult males of the four species of *Procnias*. (A) *P. tricarunculata*; (B) *P. alba*; (C) *P. averano*; (D) *P. nudicollis*. The three outermost primaries of the right wing are shown. Note that not only does the shape of the feather tip agree in *P. tricarunculata* and *P. alba*, and in *P. averano* and *P. nudicollis*, but also the ninth primary is the most modified in the first pair, and the eighth primary in the second pair. There is some individual variation in the degree of modification of the feathers.

The calls of the males are alike in so far as both have a disyllabic call of which the second note is slightly higher-pitched than the first.

DISTRIBUTIONAL HISTORY

All four species have an essentially montane distribution. *P. nudicollis* and *P. tricarunculata*, living at the highest latitudes, undertake extensive vertical migrations, breeding in montane forest and descending to lowland forest in the off-season. *P. alba* and *P. averano* wander to some extent, perhaps regularly, from the montane areas which are their headquarters, for in spite of comparatively little collecting and rare field observation there are a number of records of undoubted stragglers (Figure 3). The montane distribution, and the complete absence of the genus from the Andes, except for the eastern spur of the range in Venezuela and extreme eastern Colombia, strongly suggest that the genus originated in highland forest of the Guiana shield or some part of eastern Brazil.

Figure 3 shows the present distribution of the genus, so far as known. It is rather unlikely that further collecting will substantially modify the picture, except perhaps in the area where the ranges of *P. alba* and *P. averano* meet (see below); indeed it is unfortunately more likely that with the deforestation of eastern Brazil and Central America *P. nudicollis* and *P. tricarunculata* no longer exist in many areas where they formerly occurred, while the survival of the eastern population of *P. averano* is gravely threatened, if indeed it still exists (see notes to Figure 3).

If the relationships of the species are as suggested in the preceding section, it is likely that the original split was into an eastern and a western form. The subsequent split of each daughter-form into two species must have involved extensions of ranges and possibly also interactions between the products of the original split. Any reconstruction is of course highly speculative, but the following is suggested as the most likely (Figure 4).

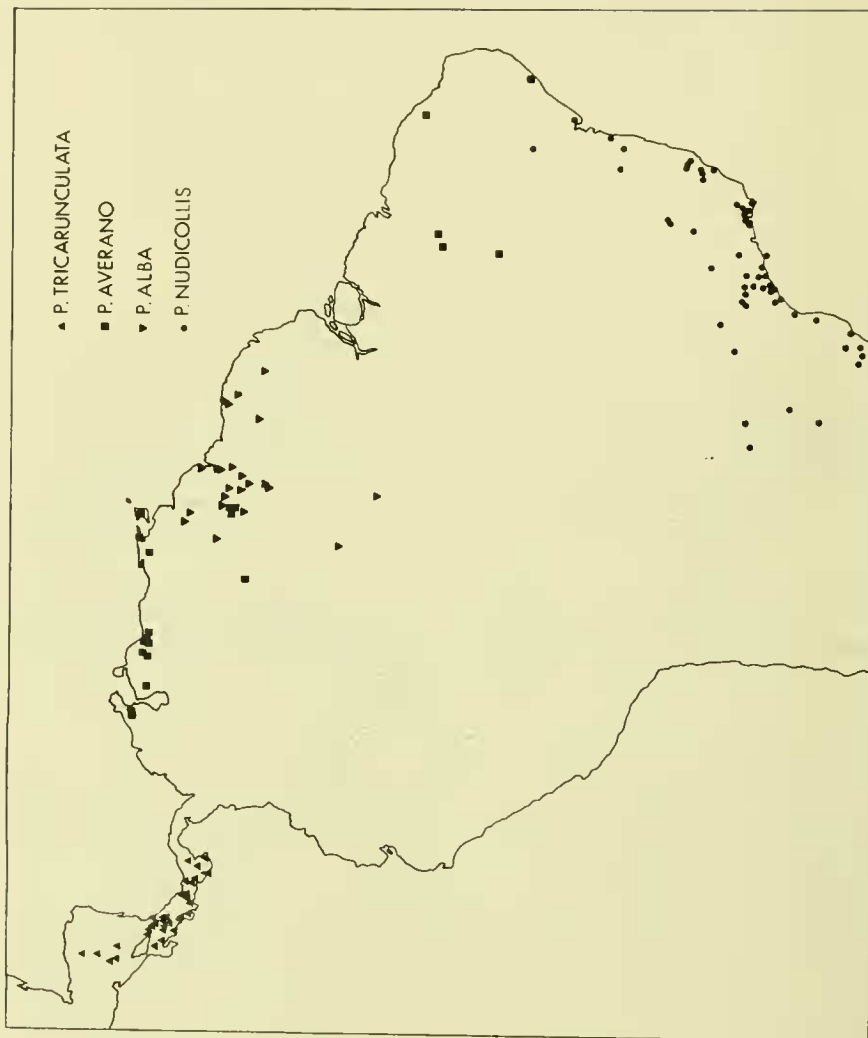
The original split probably gave rise to two stocks, one in eastern Brazil and the other in the Guiana highlands. This is based on the fact that three of the four species occur in northern and eastern parts of South America; while the presence of an isolated species in Central America and the complete absence of the genus from the main chain of the Andes (a unique distribution in the Cotingidae) strongly suggest that the Central American population reached its present home by long-range colonization.

The eastern form probably split into two – *averano* in the north, *nudicollis* in the south – during a period of aridity, when the highland forests of northeastern Brazil were isolated (as they now are) from those of eastern coastal Brazil. The western form, as already suggested, meanwhile probably split into two by establishing an isolated offshoot in Central America. The result of these processes would have been a chain of four species arranged in a phylogenetically 'logical' order from east to west.

The present distribution, however, is not so simple. *P. averano* has two widely separated populations, with *P. alba* interposed between them in the Guiana highlands, where on the present hypothesis it is likely to have originated. One may suppose that the western population of *P. averano* reached its present area by a long-range colonization from the east; and this may well have been very recent, since the eastern and western forms constitute only slightly marked subspecies. Further support for this interpretation is derived from the fact that the Venezuelan north coastal mountains have clearly not been an evolutionary centre of any importance in the Cotingidae; no species has its centre of distribution in this area, in marked contrast to the Guiana highlands and eastern Brazil.

The suggestion put forward by Sneath (1928 : 539), that the present distribution of *P. averano* north and south of the Amazonian lowland forest indicates that at some time in the past dry savanna woodland was continuous across what is now the lower Amazon valley, seems much less likely. He was impressed by the occurrence of *P. averano* in rather dry, highly seasonal forest in northeastern Brazil; but this is not generally typical of the habitat of bellbirds, and it seems more likely that, in the area where it still occurs in northeastern Brazil, *P. averano* is restricted to the richest montane forest which remains, the whole of this part of the continent having probably suffered from recent desiccation.

There remains the problem of the present relationship between *P. alba* and *P. averano* in the area where they adjoin. Phelps & Phelps (1963) give the altitudinal range of *P. alba* in Venezuela as tropical, up to 1000 m, and that of *P. averano* as tropical and lower subtropical, from 360 to 1600 m. The altitudes given for *P. averano*, however, include the north coastal mountains, where *P. alba* does not occur. In the southeast of the country, where the two species meet, there is only slight

FIG. 3. Distribution of the genus *Procnitis*.

evidence that they differ in altitudinal preference ; but the data are so fragmentary that further collecting or observation may well alter the picture, and it may even turn out that on Roraima and perhaps other mountains *P. alba* occurs at low altitudes and is replaced at higher altitudes by *P. averano*. The records available at present are as follows :

<i>Procnias alba</i>		<i>Procnias averano</i>	
Roraima	1100 m	Roraima	1100-1300 m
Auyan-tepui	1100-1500 m	Acopan-tepui	1200-1600 m
Cerro Tomasote	500-600 m	Uei-tepui	1300 m
Altiplanicie de Nuria	460 m	Maniña head-waters	700 m

If, as suggested above, *P. averano* 'leap-frogged' over *P. alba* to establish itself in the coastal mountains of Venezuela, subsequent expansion of the newly established population would have brought it into contact with *alba* in the east. That they now apparently replace each other with little or no overlap, in spite of the fact that individuals must frequently straggle into each other's range, strongly suggests that they are ecologically or ethologically incompatible. The two are nearly the same size and feed in the same way, so that the usually accepted conditions for competition exist ; but it is not easy to see how competition for food could operate, when many other species share all of their foods, which are probably often, perhaps usually, locally superabundant (Snow 1971). The possibility of behavioural interactions unconnected with food supply should be borne in mind.

FIG. 3

Sources and notes.

P. tricarunculata. Records from Hellmayr (1929) Slud (1964) and Monroe (1968), supplemented by specimens in museums of Paris, New York, Washington, Yale and Philadelphia. Not all records can be shown in Panama and Costa Rica, but the limiting records are shown.

P. averano. Records from Hellmayr (1929), Pinto (1944, 1954), Meyer de Schauensee (1950), Camargo (1957), Phelps & Phelps (1962, 1963) and specimens in U.S. National Museum, Washington. The species just extends to Colombia (Montes de Oca, Colombia-Venezuela border) and to Brazil (Cotinga River and Cerro Uei-tepui (El Sol) on the Venezuelan border). The only record from Guyana based on a specimen (Adaroo River, Phelps coll.) is omitted, as the locality is untraceable. A sight record from Guyana (Kanuku Mountains, within the range of *P. alba*, March 1970; pers. obs.) is also omitted.

For the northeastern population the records plotted represent all that are known, except for the original specimen collected in Pernambuco, without exact locality, by Marcgrave (Pinto 1944).

P. alba. Records from Hellmayr (1929), Haverschmidt (1955, 1968), Phelps & Phelps (1963) and Snyder (1966). The two far southerly records (Barcelos and 20 miles up the Rio Negro from Manaus) almost certainly refer to stragglers. Occasional stragglers (not shown) have also occurred in Trinidad, within the range of *P. averano* (Snow 1970). Wallace's sight record near Belém (Pará) is puzzling, since it is so far outside the normal range, and is also omitted. Without doubt the species occurs more widely in the south of Guyana and Surinam than is shown. For French Guiana there appear to be no more exact records than the general locality 'Cayenne', used in the older literature, and a single symbol is placed in a likely locality in the centre of the country.

P. nudicollis. The great majority of the published Brazilian records are plotted (Hellmayr 1929, Pinto 1944), and all those published for Paraguay and Argentina (same authors, Laubmann 1940). Additional Brazilian records are based on specimens in the museums of Belém, Rio de Janeiro, São Paulo, New York, Washington, Philadelphia and Leiden. Not all records are shown for the area where records are concentrated in the southeastern Brazilian coastal region.

The distribution of *P. nudicollis* at its northern limit is poorly known. The most northerly record but one was collected in the vicinity of Bahia (by R. H. Beck, specimen in New York), but the exact locality is not known.

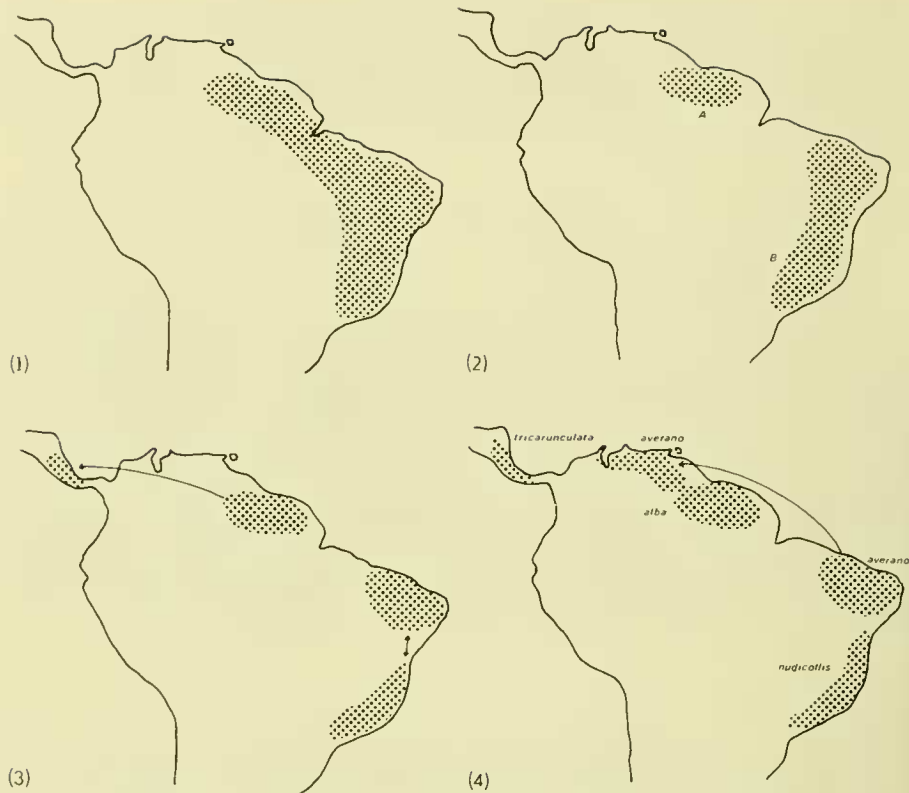


FIG. 4. Hypothetical distributional history of the genus *Procnias*. (1) Ancestral form in some part of northeastern South America. (2) First split, leading to one population in the Guiana highlands and the other in the eastern Brazilian highlands. Subsequent differentiation of adult males: A, wattles concentrated round beak, few in number; throat feathered; B, wattles concentrated on throat; throat otherwise bare. (3) Later splits, probably by long-range colonization of Central America by the western population, leading to differentiation of the four presently existing species. (4) Long-range colonization of northern Venezuela by *P. averano*.

DISTRIBUTION IN RELATION TO FOOD TREES

It is probable that the size, and especially the gape size, of bellbirds has evolved in close relation to the size of the fruits on which they feed, and that their generally montane distribution is similarly related to their food trees. It is not possible to do more than suggest these connections and back up the suggestion with fragmentary evidence, until more complete data are available on the tree families on whose fruit bellbirds mainly feed. The importance for specialized neotropical frugivorous birds of three plant families (Lauraceae, Burseraceae and Palmae) has been discussed in an

earlier paper (Snow 1971). The first two of these families are important in the diet of *P. averano* in Trinidad (Snow 1970); in particular, the young are fed largely on lauraceous fruits, and the breeding season coincides with the time when most species of Lauraceae are in fruit. Palm fruits, on the other hand, are mostly too large or too firmly attached for bellbirds to be able to take them (they are important in the diet of some of the very large cotingas usually known as fruit-crows). There is no detailed information on the diet of the other bellbirds, but Skutch (1969) mentions the importance of the Lauraceae in the diet of *P. tricarunculata*.*

It is unfortunately the case that the Lauraceae and Burseraceae are taxonomically difficult families. The Lauraceae, in particular, contains very many species with relatively slight morphological differences between them. This may, in fact, be a direct consequence of interspecific competition between them for dispersal by birds, which would be expected to result in differences in fruiting seasons (Snow 1965) and perhaps other ecological characters, while the fruit characters would be held within acceptable limits of size, shape and nutritional quality.

Like other cotingas, bellbirds swallow fruits whole. The fruits must therefore be able to pass between the rami of the lower jaw, which are bowed markedly outwards, doubtless as an adaptation for swallowing fruits of large size. It is this outward bowing of the rami of the jaw, combined with the rather low crown, that gives the bellbirds their frog-like appearance, already mentioned. The maximum size of the fruits which they can swallow can thus be assessed directly from the skull, if some allowance is made for the thickness of the tissues overlying the bone. (A similar measurement for manakins of the genera *Manacus* and *Pipra* gave figures which agreed very closely with the upper limit of size of fruits seen to be taken in the field.)

The single available skull of *Procnias*, an unsexed but almost certainly adult male *P. nudicollis*, can 'swallow' fruits of diameters up to 22 mm. The width of the gape measured externally on study skins of this species is 24–26 mm in males and 21–23 mm in females. On the same basis, and assuming that the measured skull is of average size, measurements for all four species give the following maximum diameters of exploitable fruits:

	males	females
<i>P. alba</i>	24–27	20–21
<i>P. averano</i>	22–24	19–22
<i>P. nudicollis</i>	21–23	18–20
<i>P. tricarunculata</i>	21–23	19

Table 2 shows that the four species of bellbirds are each able to eat almost all the known species of lauraceous fruits in their respective habitats. In French Guiana, for instance, only one species of the Lauraceae has fruits much too large for *P. alba*,

* Pelzeln (1868) most surprisingly recorded snails in one of three stomachs of *P. nudicollis* examined the other two contained only fruit remains; and Burmeister (1856) gave the food of this species as fleshy fruits, with insects an additional item ('wohl nur als Zukost' – merely as seasoning). In view of the more recent evidence for an exclusively fruit diet these early records might seem questionable; yet the extinct frugivorous pigeon of Mauritius, *Alectroenas nitidissima*, was said to eat molluscs as well as fruit (Goodwin, 1970), and other mainly frugivorous pigeons certainly do so. Possibly the low calcium content of a pure fruit diet requires an occasional supplement from other sources, perhaps especially for egg-laying females.

and this is the well-known Greenheart *Ocotea rodiaei*, whose fruits have a woody pericarp and are obviously adapted for dispersal in quite a different way. Again, all but one of the known Panamanian species for which Allen (1948) gives measurements are within the range that can be taken by *P. tricarunculata*, and their upper limit is exactly the bellbird's upper limit.

TABLE 2

Diameters of fruits of the Lauraceae from Panama, Trinidad, French Guiana and S.E. Brazil and maximum size of fruits that can be swallowed by the four species of *Procnias* occurring in these areas

Area	Panama	Trinidad	French Guiana	S.E. Brazil	
<i>Procnias</i> sp.	<i>tricarunculata</i>	<i>averano</i>	<i>alba</i>	<i>nudicollis</i>	
Maximum diameter of exploitable fruit	♂ 21-23 ♀ 19	♂ 22-24 ♀ 19-22	♂ 24-27 ♀ 20-21	♂ 21-23 ♀ 18-20	
Number of species of Lauraceae with fruits of diameter (mm)	30 + 27 25 23 22 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5	- 1 - - 1 3 - 2 1 1 3 - 1 1 3 6 2 4 2 2 1	- - - 1 1 - 1 - - - 1 - 5 4 3 4 1 1 - - -	1 - - - 1 - - 2 - - 4 3 2 5 2 2 1 6 4 4 5 -	- - - - 1 2 - 2 - - 5 1 2 3 2 8 2 6 3 7 4

Notes. Botanical data for Panama from Allen (1948); for Trinidad from Marshall (1938) and personal measurements; for French Guiana from Lemée (1952-6); and for S.E. Brazil (States of Rio de Janeiro and São Paulo) from Mez (1889).

Many species of Lauraceae are found at all altitudes in neotropical forests, but there is little doubt that they are numerically more important in montane than lowland forest. For Trinidad, the lists of trees per 100 acres in different forest types given by Beard (1946) show that in six faciations of lowland forest ('Evergreen Seasonal Forest') there are 4-6 species of Lauraceae in totals of 87-104 tree species; while in Lower Montane Rain Forest, which grows at c. 250-800 m above sea level, there are 10 species of Lauraceae in a total of 87 tree species. A recent monograph on the lauraceous genus *Persea* (Kopp 1966) shows that in Central America, where this genus is strongly represented, the majority of the species have been recorded between 1000 and 2000 m above sea level, and rather few below 1000 m. Sketch

(1969) draws attention to the confusing variety of species of Lauraceae in the montane forests of Costa Rica. By contrast, only two species of *Persea* are recorded by Kopp from the whole of the vast lowland Brazilian State of Amazonas.

To what extent the bellbirds' breeding seasons in areas other than Trinidad, and their seasonal movements, especially the vertical migrations in Central America and eastern Brazil, are related to the fruiting seasons of their food trees must await future investigation. The evidence available so far suggests that the trees of a few families will be found to play a key part in their annual cycle, just as they seem to have in determining their distribution and morphology.

ANNUAL CYCLE

No nest has been found of any bellbird except *P. averano* in Trinidad (Snow 1970). In spite of this, it is fairly certain that the two species which breed at the highest latitudes, *P. tricarunculata* in the north (about 9 to 14 degrees north) and *P. nudicollis* in the south (about 12 to 26 degrees south), follow the spring/summer breeding regimes that are prevalent in Central America and eastern Brazil (Skutch 1969, Euler 1867). The available moult data are difficult to evaluate, but it seems that adults begin to moult during the breeding season or immediately after it, while young birds begin a complete moult shortly before the breeding season begins. The information on which this conclusion is based is discussed more fully in a forthcoming survey of moult cycles in the family Cotingidae.

P. alba and *P. averano*, living mainly within 10 degrees of the Equator, certainly have less clearly defined seasons of breeding and moult over most of their ranges than the other two species. *P. averano* in the centre of the Northern Range of Trinidad, at the northern limit of the species' range, has a main egg-laying season in April–July and a minor season in October–November. Adults begin to moult between April and August, and young males on average considerably earlier, in March and April. The moult records for *P. alba* show no clear seasonal pattern.

After breeding, *P. tricarunculata* in Costa Rica moves down from the highland forests to the lowlands. Thus at an intermediate level Skutch (1969) records them as present chiefly in July–September and January–March, and they are recorded in the lowlands mainly in winter. Similarly *P. nudicollis* moves down to lower altitudes in the southern winter, but little seems to have been recorded in detail. All four species undertake local movements which may or may not be seasonal, apparently in connection with the fruiting of their food trees.

PLUMAGE SEQUENCES

Male bellbirds take a long time to acquire fully adult plumage, and in the course of acquiring it pass through a succession of individually highly variable plumage stages. The moulting process is probably slow, and it is often found that the colour of the newly acquired flight or tail feathers changes progressively along the row, showing progressively more adult characters. Often too the base of a feather is markedly more adult in colour than the tip. Much of the variability appears to result from a variation in the relative timing of the moults and the changes in the bird's hormonal

state. Another source of variability is the haphazard replacement of wing-feathers, especially secondaries, out of the normal sequence. Furthermore, it is not uncommon for the wing moult to be arrested before it is complete. It is not possible to tell from a study of skins whether, after being arrested, moult is resumed from the point where it stopped, but it is certain that a moult sometimes begins, or is resumed, at some intermediate point in the normal sequence. Feathers or parts of feathers that are transitional between juvenile and adult type, especially those transitional to white, tend to show a 'peppered' effect, being finely spotted with the remnants of the dark colour that is being lost.

Because of their more synchronized annual cycle, it is much easier to work out the time of the plumage changes in *P. tricarunculata* and *P. nudicollis* than in the other two species. For the purpose of working out the changes from juvenile to adult male plumage, it is assumed that all *P. tricarunculata* were hatched in June and all *P. nudicollis* in December (see previous section). It is unlikely that this assumption will introduce an error of more than two months in ageing a specimen.

Assuming these hatching dates, the evidence from dated specimens shows that the sequence and timing of plumage change are very similar in these two species (Figure 5). Young males undergo a succession of complete annual moults, beginning when

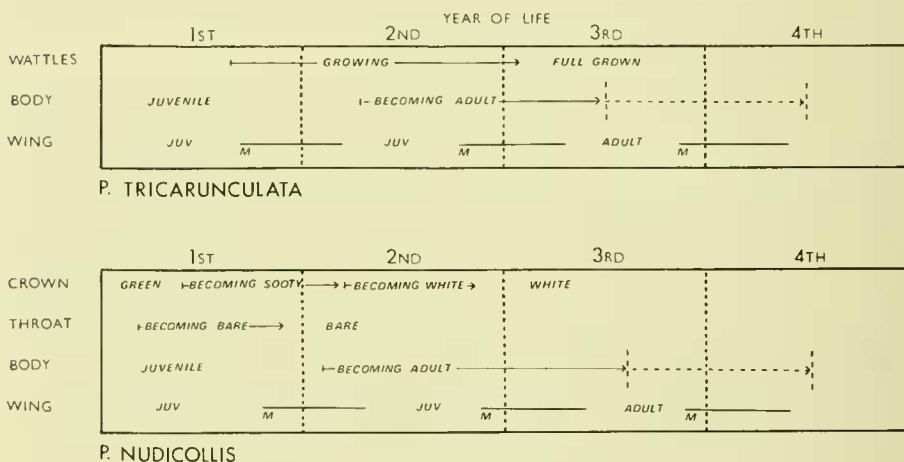


FIG. 5. Generalized time-table of acquisition of adult plumage by males of *Procnias tricarunculata* and *P. nudicollis*. Body plumage: the broken line represents the period within which fully adult plumage is acquired (individually variable). Wing: the lines labelled M indicate periods of moult of the flight-feathers.

they are a little under a year old. At the first complete moult the wing and tail are replaced again by juvenile feathers; the head and body feathers are replaced, variably and perhaps more gradually than the wing and tail, by feathers of more adult type. In some birds, the last wing and tail feathers to be replaced also show a

tendency towards adult colouration. When the bird is a little under two years old another complete moult leads to the assumption of wing and tail feathers of adult or nearly adult type, and the head and body also become nearly adult in colour. In some individuals completely adult body plumage is acquired without a further wing moult, presumably by gradual replacement; in others, the fully adult plumage is not acquired until after the third complete moult. The replacement of odd wing and tail feathers between these complete moults may result in irregularities, with a few feathers of more adult type than the rest.

In *P. tricarunculata*, the wattles begin to grow when the male is between six months and a year old (assuming hatching in June), and they evidently grow fast, those at the gape much faster than the central one, since by the end of the first year they may be up to 20 mm long. They do not then grow much more during the following year. In *P. nudicollis* the male's throat becomes bare in the course of the first year.

It is difficult to investigate the body moults which do not involve a colour change, but there is probably a complete body moult in the first few months of life. In *P. nudicollis* the crown becomes sooty-black in this period, to be replaced by white in the first months of the second year.

In *P. averano* and *P. alba* the less well-synchronized annual cycle (which may also differ in different parts of the species' ranges, according to the regime of wet and dry seasons) and more frequent irregularities of moult sequence make a reconstruction of plumage changes more difficult; but the observed changes in plumage in a male *P. averano* in Trinidad, of known age (Snow 1970), provide a useful time-scale for part of the juvenile period. It seems that the plumage sequence and timing are very much the same as in *P. tricarunculata* and *P. nudicollis*. There is a succession of full moults, apparently starting when the bird is nearly a year old. After the first, the wing and tail are still of juvenile type, after the second they are sub-adult, and after the third fully adult in colour. In *P. averano* an early moult, probably of the whole head and body, leads to the assumption of a sooty crown, and this is replaced by the brown crown of the adult during the second year. After the first full moult the back also becomes sooty in colour rather than green, and later often grey-brown, before the very pale grey adult colour is acquired. The change is variable and probably depends on the relative timing of hormonal changes and of moults.

In *P. averano* the pale juvenile throat feathers are replaced by sooty feathers at about the same time as the sooty crown is acquired. The wattles probably develop at the age of about a year; in the Trinidad juvenile they were just visible, in the field, at the age of 16 months. In the only specimen of *P. alba* examined at the appropriate stage, the wattle was present but short when the bird was half-way through its first wing moult, presumably at an age of just over a year.

THE WATTLES

The age at which the wattles first appear has just been mentioned. In all three of the species with wattles, they begin to grow in the young male while the plumage is still wholly juvenile, and are a good size, though probably not full-grown, by the time that the adult plumage is complete. The wattles are bare, shiny and blackish

in *P. tricarunculata* and *P. averano* ; in *P. alba* the single wattle is black and is sparsely covered with small white star-like feathers. The bare skin of the throat of *P. nudicollis* is greenish ; it is not completely bare, but is sparsely covered with black bristles. Similar bristles grow between the wattles on the throat of *P. averano*.

The histological structure of the wattles has not been investigated. Schomburgk (1848) asserted that the wattle of *P. alba* is hollow and muscular, and in direct communication with the palate, and that it can be inflated at will. Waterton (1824) had earlier said much the same thing. As a result the older illustrations of *P. alba* usually show it with the wattle standing straight up like a unicorn's horn. From close observation of a captive bird, Quelch (1892) refuted Schomburgk's assertion, describing the wattle as made up of fine elastic tissue. Little can be added so far as the histology goes, except that the wattle must also contain muscle fibres, as Salvin (1865) suggested for *P. tricarunculata*.

The first good account of the wattles in life was given by Quelch. Writing of a male *P. alba* in captivity in British Guiana (Guyana), he wrote : 'When the bird is about to utter its characteristic notes, this appendage slowly becomes greatly elongated - to as much as five inches, I have observed at times. At the conclusion of the note, the organ may remain extended till the next note, or it may be partially retracted ; but when a long interval takes place, the structure is always allowed to shrink up to about half an inch or an inch in length, at will ; and it then hangs against the beak.' Similarly Snow (1961) observed that when a male *P. alba*, observed in the wild, had finished a bout of calling the wattle contracted to about a third of its former length before the bird flew off to feed. Crandall (1948) also reported that in a captive *P. tricarunculata* the wattles enlarged to about three times their usual dimensions when the bird was calling.

The mass of wattles on the throat of *P. averano* does not alter so noticeably when it is calling ; but they are made more conspicuous by the erection of the feathers of the upper breast, which push the bird's black 'beard' forwards (Snow 1970). It is probable, however, that in this species too the wattles can be extended by muscular action. Thus W. G. Conway (*in litt.*) noted that in a captive *P. averano* in the Bronx Zoo, New York, the wattles appeared shrivelled up when it stopped calling and began to moult.

It seems clear that the display of the wattles, in all three species, is closely connected with calling, and there is no doubt that the main function of all the male's displays is to attract females to the calling perch, on which mating takes place (Snow 1970). Presumably the wattles, in combination with the striking plumage and associated behaviour, play an important part when the female is at close quarters ; certainly in *P. averano* the male's performance appears to rivet the female's attention. Crandall (*loc. cit.*) reported that a female *P. tricarunculata* in captivity appeared to be attracted by the dangling wattles of a male and at least once reached forwards as if to peck at them. This is almost certainly not normal behaviour, since in *P. averano*, and probably also in *P. alba* (Snow, *in press*), the male and female stay two or three feet apart during courtship, until the male leaps, with an explosive call, onto the female. Nevertheless, the wattles may perhaps be regarded as structures analogous to the dangling silky fringes of the modified secondary feathers of the Cock

of the Rock *Rupicola rupicola*, which attracted a courting female to lean forward and nibble at them (Snow 1971).

The evolution of extensible wattles as a result of sexual selection has brought with it a concomitant disadvantage, though probably not a serious one, for the males of the two species whose wattles grow from the base of the beak. Crandall mentioned that the long wattles of a captive *P. tricarunculata* were a positive nuisance to the bird when it wanted to feed; and Snow (1961) noted that a male *P. alba*, when calling, had to ensure that its wattle was hanging down on the right side before it could begin one of its calls, which involved swinging the head to the left.

VOICE

Male bellbirds utter what are perhaps the loudest of all bird calls; the females and nestlings, at least of *P. averano*, are almost or completely silent (Snow 1970). The main characteristics of the calls of the four species are described and illustrated in the following sections, which are followed by a brief discussion of functional, mechanical and evolutionary aspects of the calls.

Procnias averano

Males of the Venezuelan population have three distinct calls: a single, very loud *bock* (Plate 1(A)); a repeated, less loud *tock, tock, tock . . .* (Plate 1(B)); and a more musical, double *kay-kong, kay-kong, . . .*, repeated more slowly than the *tock, tock, tock* (Plate 1(C)). The single *bock* is remarkable for the rather even distribution of energy over a wide frequency range, with the emphasis on the second harmonic, and for the very sudden beginning of the note. These features combine to give the note its sudden, unmusical hammer-like quality. The repeated *tocks* are very similar in form to the *bock*, but only two instead of six harmonics above the fundamental are apparent in the sonogram.

The double *kay-kong* is of more complex form: the main part of the first syllable is very similar in form to the *tock* but more drawn out, while the second syllable has almost all its energy concentrated at the fundamental frequency, thus producing a more musical and lower-pitched note. In the first syllable, the harmonics begin a little after the fundamental frequency is sounded. Both syllables begin with a preliminary pulse of energy whose upper frequency is intermediate between the frequency of the second and third harmonics. Exactly the same preliminary pulse is apparent at the beginning of the *tock*, where it is less distinct in time from the main part of the note, while in the *bock* it is, as it were, attached to the main part of the note, so that there is a sudden descent in pitch which is most marked in the higher harmonics.

The *bock* of the Trinidad bird (Plate 1(D)) is even more remarkable for the even distribution of energy over a wide frequency range, and for its short duration, which gives it an even duller, more hammer-like quality than the *bock* of the Venezuelan bird. The repeated *tocks* (Plate 1(E)) are simply less loud versions of the *bock*. The refinements of the beginning of the call, noted for the Venezuelan bird, are not present.

Males of the Trinidad population now use only these two calls, the *bock* and the repeated *tock*, but, as Snow (1970) has pointed out, there is good evidence that a third call was being used by the Trinidad population in 1893, when Brewster and Chapman visited the island (Brewster & Chapman 1895). This third call was disyllabic and may have been similar to the *kay-kong* of the Venezuelan population (but see footnote to p. 388). The implications of this loss of part of the repertoire are discussed in a later section.

Snethlage (1928) has given the only account of the calls of the population of *P. averano* in northeastern Brazil. He wrote: 'Zwar verfügt er nur über zwei Töne: einen schweren und einen leichteren Schlag, die den Hammerschlägen auf Eisen gleichen. Ein schwerer Schlag, kleine Pause, dann regelmässige leichte, das ist der Gesang, der zur Zeit der ersten Regen (im August–September) weithin zu vernehmen ist.' (They use only two notes: a loud and a softer note, which sound like the blows of a hammer on iron. A loud blow, a short pause, and then regularly repeated and less loud notes – that is the song, which is to be heard from afar at the beginning of the rains (August–September).)

Before uttering the explosive *bock* the bird opens its beak very wide, and the call is given when the beak is fully open (Snow 1970). Brewster & Chapman described the calling bird as throwing its head forward and downwards with a violent, convulsive jerk, but this is certainly not normal behaviour. When the repeated *locks* are being uttered the beak remains open, the lower mandible merely moving down and then upward again with each note.

Procnias nudicollis

Two calls are uttered: a single *bock* (Plate 2(A)) and a repeated call (Plate 2(B)). The *bock* is extremely similar to that of *P. averano*; the repeated call is probably homologous with the repeated *tock* of *P. averano*, but it is of most peculiar structure: a less loud but otherwise apparently identical version of the *bock* is followed, about 0.08 second later, by a very loud and pure high-pitched note, exactly an octave above the fundamental frequency of the first note. The two very different and partly overlapping notes give the impression of a hammer striking an anvil a glancing blow so that it rings.

Greenewalt (1968) presented an oscillogram (time-amplitude diagram) of this call, together with a time-frequency plot, giving it as an example of a call in which two independent sound sources must be involved. This aspect of the call is discussed more fully in a later section (p. 387).

When preparing to utter the explosive *bock*, the bird is described as opening its mouth very wide, perhaps inhaling; it then bows forward as the *bock* is uttered. The continuing, repeated notes are accompanied by coordinated nodding or slight bowing (manuscript notes by R. Ward, who made the recordings used for the sonograms).

Procnias alba

Of the four bellbirds, this species has by far the most musical voice, and is the one which gives the genus its popular name. There are two calls: a double *kong-kay*

(Plate 2(C)) and a long drawn-out *do-i-i-i-ing* (Plate 2(D)). This second note, attenuated to a silvery chime as it filters down through the forest trees, is among the most beautiful sounds of the Guiana forests.

The two notes of the *kong-kay* are similar in structure, but the second is a little higher pitched than the first (fundamental frequencies of about 1.8 and 1.7 kHz respectively). Though it is difficult to be certain of this, it seems from detailed inspection of the sonograms that the two overlap in time, and thus are presumably produced by two independent sound sources.

The utterance of the double *kong-kay* is sometimes accompanied by a characteristic movement (Snow 1961). The bird turns sharply to the right to utter the first syllable; then with beak still wide open it rotates the body rapidly through an arc of about 100 degrees, to make the second note facing to the left. The wattle normally hangs down to the right of the beak, so that it flies out horizontally as the bird swings to the left. If it happens to be hanging down on the left side, the bird manoeuvres it to the right side before calling.

The drawn-out *do-i-i-i-ing* is a pure note of very even pitch, with a single harmonic. It is usually more or less clearly broken into two notes (Plate 2(D)), the second syllable being shorter and dying away with a slight tremolo. Because it tends to be disyllabic, it has been written as *do-rong* (Quelch 1892, Snow 1961).

Quelch's detailed description of the calling of a captive male of *P. alba* in Guyana is worth quoting in full, since the way in which the air is inhaled and the movements associated with the calls are relevant to the problem of the two sound sources, discussed in a later section (p. 387). 'When the appendage is fully elongated [see earlier, p. 382, for distension of the wattle], the bird suddenly inflates its lungs, right and left, by inhaling - almost by a swallowing action - two great draughts of air; but the method by which this is done depends upon which of its two characteristic notes it intends to utter. When the notes "Kong-Kay" are uttered, the action of inflation has been performed by two distinct inhalations of air, one with the head turned to the right and the other immediately after to the left. At the moment of utterance of the notes, the head is turned to the right for the "Kong", and then suddenly - so suddenly that it almost startles the observer - the head is swung round to the left for the "Kay", which is issued with a strikingly loud, piercing and metallic ring or clang - so loud and shrill indeed that, if the observer is close by, the ears are actually deafened for the moment by the sharpness of the sound.

'When, however, the sweet, musical, and deeply-toned bell-like notes "Do-rong" are about to be uttered, the bird is observed simply to hold its head forward, and to make two distinct gulps of air; and then, holding its beak upwards and slightly extending its neck, the notes are rolled out, as it were, with full voice and roundness and resonance.'

Procnias tricarunculata

Of the four bellbirds, this species has the least highly developed repertoire. Skutch (1969) has given the fullest account of its voice. There are apparently only two distinct notes, one 'loud and strong but dull and throaty' (*buck*), the other much sharper and higher in pitch (*wheat*). The sonograms show less difference between these two

notes than might be expected from Skutch's description (Plate 2(E)), but they are in fact quite distinct. The *buck* has much of its energy centred, rather diffusely, round frequencies of about 1.75 and 3.5 kHz, with some energy at very low frequencies. This frequency distribution presumably accounts for the dullness of the tone, which Skutch likens to a wooden clapper, while the roughness of the sound probably comes from the irregular pattern of frequencies at the beginning of the note. The *wheat*, on the other hand, has its main frequency band about 0.3 kHz higher than that of the *buck*, has no very low frequencies and shows an orderly series of diminishing harmonics.*

It is clear from Skutch's account that, although the two notes are commonly uttered in succession, to form the phrase *buck wheat*, they are also given in every possible combination. The significance of this lack of organization in calling behaviour is discussed in a later section (p. 388).

FUNCTION OF THE CALLS

The epigamic function of these very loud calls has already been briefly mentioned (p. 369). There is no doubt that they are advertising calls, and one of the means by which males attract females to their display perches. Why such a very loud call should have evolved in this genus is not clear; but it should be noted that many forest birds, in which the males display at traditional sites, have loud advertising calls. In the Cotingidae very loud calls, though of a different kind from those of the bellbirds, are uttered by males of other large species, in the genera *Tijuca*, *Perissocephalus*, *Pyroderus*, *Cephalopterus* and *Lipaugus*. Males of other genera are less noisy, but these advertise themselves from a distance by making themselves visually conspicuous. The bellbirds are peculiar in having two extremely effective methods of making themselves conspicuous from a distance. A mainly white bird calling very loudly from an exposed tree-top – a usual calling perch – could hardly advertise itself more effectively. At least in *Procnias averano*, the later stages of courtship display are carried out beneath the canopy of the forest, on comparatively low perches, and are silent except for the loud *bock* which accompanies the mating leap.

One of the ways in which vertebrates can locate sounds is by comparison of the time of arrival of the sound at the two ears. This is possible only if the sound begins or ceases abruptly (Marler 1955). The extraordinarily sharp beginnings of the bellbirds' calls should therefore make them especially effective in this respect, and in fact a bellbird calling at a distance can be accurately located by the human ear, as long as one is in the open. It is, however, rather difficult to locate a calling bellbird if one is under the forest canopy, probably because the sound is reflected with varying degrees of strength from the trees all round.

MECHANISM

The vocal mechanism which enables bellbirds to produce explosively loud calls of varied structure and complexity has not been fully elucidated. Greenewalt

* In an earlier account Ridgway (1905) described the call as 'like a heavy stroke with a hard mallet on a hollow log of hard wood followed immediately by a wonderfully loud, clear and prolonged whistle'. This is endorsed by Slud (1964); but the only available recording matches Skutch's description closely, since the *wheat* is not prolonged. Perhaps there is local or even individual variation in the calls of this species.

(1968) has discussed the physical basis of sound production by the avian syrinx and gives the reasons for believing that the sounds produced depend on the vibration of syringeal membranes alone, and that little or no importance is attributable to the resonance of the trachea, or to modulation of the sounds in the larynx. Greenewalt concluded from the anatomical evidence, and from early experimental evidence, that the only membranes actively involved in sound production were the two internal tympaniform membranes. Thorpe & White (1969), however, have pointed out that the external tympaniform membranes are also involved, at least in some species.

It has been known for a very long time (Herissant 1753) that the production of sound by the syrinx depends on air pressure in the interclavicular air sacs which surround the syrinx, and Rüppell (1933) confirmed this with experiments on an isolated syrinx. Greenewalt took the theoretical analysis much further, and showed that 'high amplitude, for phrases rich in harmonic content, must be associated with increased pressure in the clavicular sac'. Since the calls of bellbirds are both rich in harmonics and extremely loud, it seems certain that they must build up an unusually high air pressure in their interclavicular air sacs. Discussing the relationship between pulse length and harmonic content, Greenewalt further pointed out that 'the more nearly one approaches a simple pulse the more terms one will find in the harmonic spectrum. The extreme case (a sharp pulse of very short duration) will produce a harmonic spectrum containing an infinite number of terms at constant amplitudes.' The single very loud calls of bellbirds perhaps illustrate this principle more clearly than any other bird calls.

Both *P. alba* and *P. nudicollis* utter calls in which two separate sound sources appear to be involved. The existence of two separate sound sources in birds' calls has been dealt with at length by Greenewalt, who considered that the right and left internal tympaniform membranes are responsible, acting independently under the influences of their separate musculature and innervation. This interpretation has been questioned by Thorpe & White (*loc. cit.*). The description of the calls of the four bellbird species, given above, can add nothing to this highly technical controversy. The behaviour associated with the double call of *P. alba* does, however, suggest the possibility that the production of sound by two vibrating membranes may be linked with the exhalation of air from the two bronchi successively. In the literature on the working of the avian syrinx there appears not to have been any serious suggestion of independent operation of the two lungs and bronchi; but this would seem to be mechanically more efficient than their obligatory simultaneous operation in the case of sound produced independently by the two internal tympaniform membranes, since the flow of air from the right bronchus, for instance, would be largely wasted if the left membrane alone were being activated. Quelch did not suggest it, but his account of the calling of *P. alba*, quoted above, suggests the possibility that the turning of the head to right and left might be linked with the asymmetrical functioning of the bronchi and lungs.

EVOLUTION OF THE CALLS

The characteristics of the calls which suggest the phylogenetic division of *Procnias* into two pairs of species have been briefly mentioned on pp. 371-372. *P. averano*

and *P. nudicollis* both have a single very loud monosyllabic call, the *bock*, of very similar structure in each. Both also utter a less loud, regularly repeated call, in structure very similar to the *bock*, except that in *P. nudicollis* there is a second, high-pitched element in the call, which is missing in *P. averano*. Both *P. alba* and *P. tricarunculata* utter a disyllabic call, of which the second note is higher-pitched than the first, but there the resemblance ends; the two parts of the call of *P. tricarunculata* are not so closely coordinated as they are in *P. alba*, and the quality of the calls differs in the two species.

Snow (1970) described how a male *P. averano* in Trinidad, colour-ringed as a nestling, had still not perfected its call when it was over two years old. It seems probable that a slow learning process is involved in the achievement of the fully adult call by young birds, and it may well be that the presence of calling adults is necessary. If this is so, some elements of the full vocal repertoire might well be lost in a very small, isolated population if for some reasons the numbers sank very low and included few or no old males. Snow (*loc. cit.*) suggested that this may account for the loss, in the Trinidad population of *P. averano*, of an element present in the vocal repertoire of the Venezuelan birds.* In the case of long-distance dispersal, leading to the establishment of a new isolated population, this is even more likely to be accompanied by a reduction of the vocal repertoire, since dispersal most commonly involves young birds. This could account for the lack of differentiation in the calls of *P. tricarunculata*, which on quite different grounds seems likely to have arisen as a result of long-distance dispersal from some area far to the east, perhaps the Guiana highlands (Figure 4). The throaty quality of the *buck*, and the varied sequence of *buck* and *wheat* described by Skutch, are rather reminiscent of the harsh and irregular calls of young males of *P. averano*. Subsequent observations of *P. alba* in Guyana (Snow, in press) have shown that the calls of young males are very similar to those of *P. averano*. It may well be that in all four species the calls pass through very similar developmental stages before they are crystallized under the influence of the calls of fully adult birds.

SUMMARY

The genus *Procnias* is one of the many isolated and peculiar genera in the neotropical family Cotingidae. It represents the culmination of the tendency towards specialization for fruit-eating characteristic of the family, associated with marked sexual dimorphism and the emancipation of the male from the nest.

* Brewster & Chapman's description (1895) of the voice of *P. averano* in Trinidad raises some interesting questions which will never be fully answered. In addition to the calls that are easily identifiable as the same as those given by Trinidad birds today, described by Snow (1970), these two authors describe a double *tui-ting*, which certainly suggests identity with the disyllabic call of the Venezuelan population (p. 383). There were, however, some clear differences in the Trinidad call, if Brewster & Chapman's description is to be relied on. 'Each *tui* is followed closely by a metallic *ting* which sounds exactly like an echo and appears to be of about the same duration and nearly as loud as the note it supplements. The *tui* notes are given so quickly that at first it did not seem possible for the bird to produce another note between them, and it was only after repeated observations we became convinced that the *ting* was an integral part of the *tui* call.' This is not the impression given by the distinctly disyllabic and well-spaced *kay-kong* of the Venezuelan bird (Plate 1(C)); indeed it seems much more like the repeated call of *P. nudicollis* (Plate 2(B)). One can only conclude that the vocal repertoire of isolated populations of bellbirds is labile, and that new elements may be gained as well as lost.

The four species, which are almost entirely allopatric, fall into two closely related pairs, *P. averano* and *P. nudicollis*, and *P. alba* and *P. tricarunculata*. Their present distribution suggests that the ancestral stock inhabited northeastern South America, that it first split into an eastern and a western form, and that each of these subsequently split into two species.

It is probable that the bellbirds' general body size, and especially the size of the gape, are related to the sizes of fruits of trees in the family Lauraceae, which provide a great part of their food.

The acquisition of fully adult plumage by the males takes about three years. In *P. averano* at least, the adult male's calls are not perfected until the third year of life. The mechanism by which the extremely loud calls are uttered is not fully understood, but there is evidence that two independent sound sources are involved.

There is some evidence that learning is important in the acquisition of the full vocal repertoire. The isolated Trinidad population of *P. averano* lacks one of the calls of the Venezuelan population. The lack of clear differentiation in the calls of *P. tricarunculata* may have resulted from a break in learning, consequent on the presumed long-range colonization of Central America by the ancestors of this species.

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PLATE 1

Sonograms of calls of *Procnias averano*.

- A. Venezuela. The *bock*.
- B. Venezuela. The repeated *tock*.
- C. Venezuela. The repeated *kay-kong*.
- D. Trinidad. The *bock*.
- E. Trinidad. The repeated *tock*.

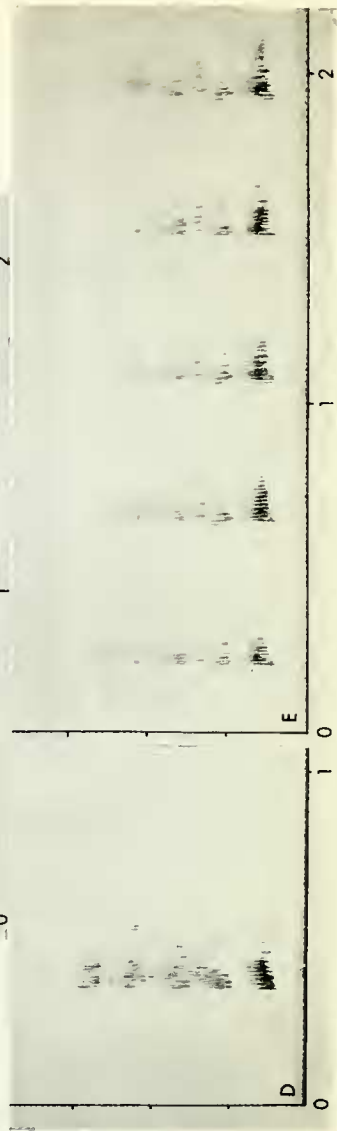
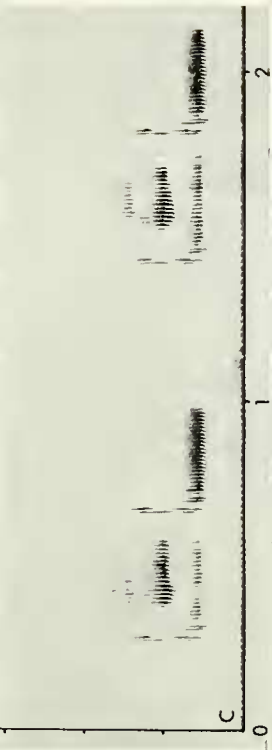
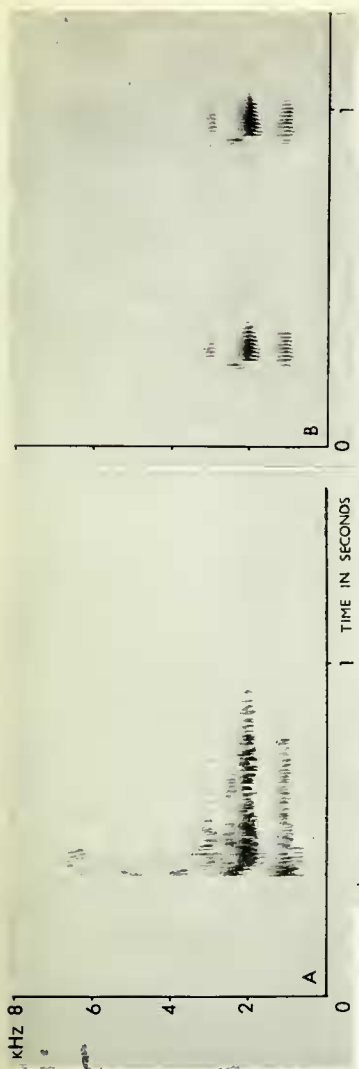
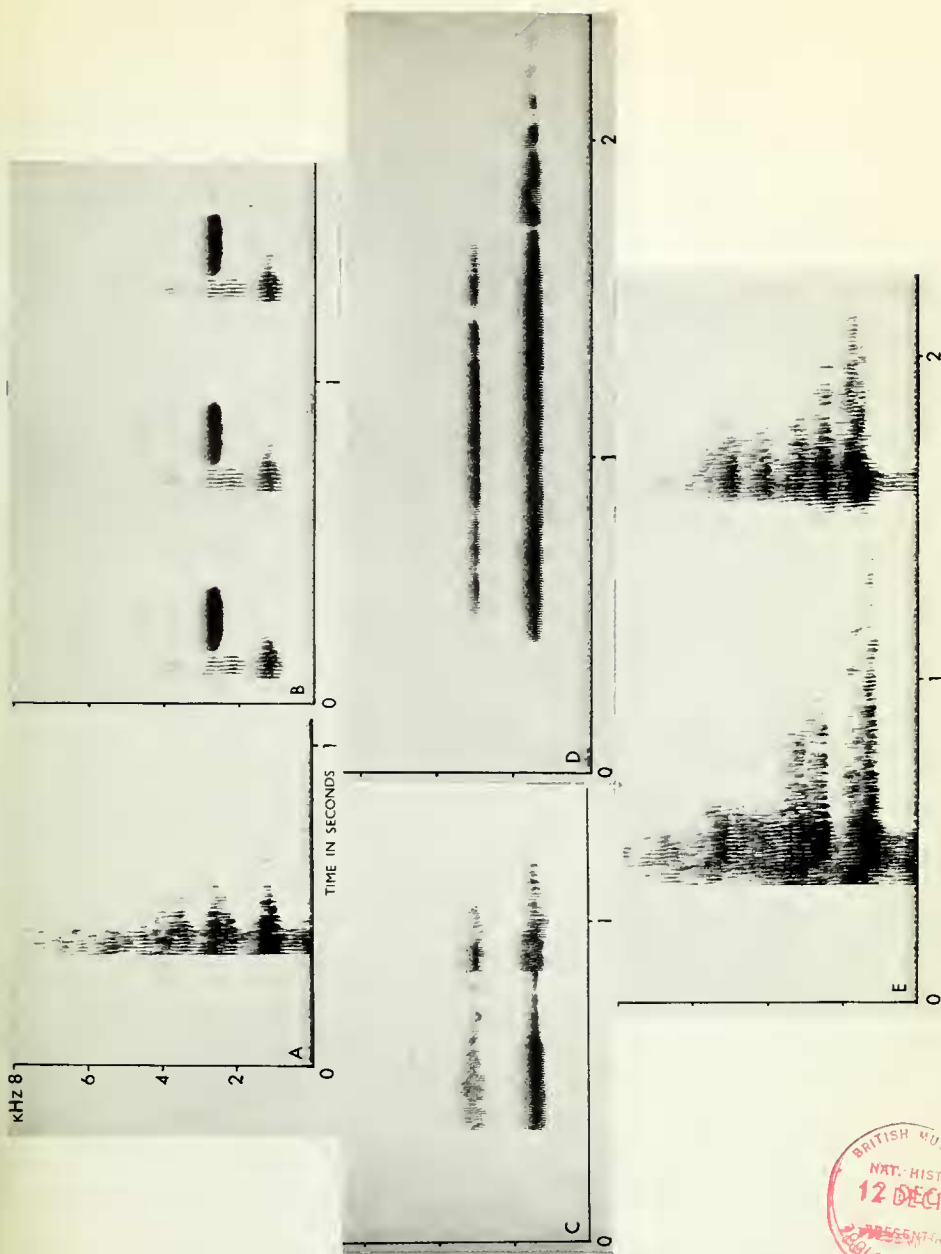


PLATE 2

Sonograms of calls of *Procnias nudicollis*, *P. alba* and *P. tricarunculata*.

- A. *P. nudicollis*. The *bock*.
- B. *P. nudicollis*. The repeated call.
- C. *P. alba*. The *kong-kay*.
- D. *P. alba*. The *do-i-i-i-ing*.
- E. *P. tricarunculata*. The *buck wheat*.



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